

## Altruism in a volatile world

Patrick Kennedy<sup>1</sup>, Andrew D. Higginson<sup>2</sup>, Andrew N. Radford<sup>1</sup> & Seirian Sumner<sup>3</sup>

**The evolution of altruism—costly self-sacrifice in the service of others—has puzzled biologists<sup>1</sup> since *The Origin of Species*. For half a century, attempts to understand altruism have developed around the concept that altruists may help relatives to have extra offspring in order to spread shared genes<sup>2</sup>. This theory—known as inclusive fitness—is founded on a simple inequality termed Hamilton’s rule<sup>2</sup>. However, explanations of altruism have typically not considered the stochasticity of natural environments, which will not necessarily favour genotypes that produce the greatest average reproductive success<sup>3,4</sup>. Moreover, empirical data across many taxa reveal associations between altruism and environmental stochasticity<sup>5–8</sup>, a pattern not predicted by standard interpretations of Hamilton’s rule. Here we derive Hamilton’s rule with explicit stochasticity, leading to new predictions about the evolution of altruism. We show that altruists can increase the long-term success of their genotype by reducing the temporal variability in the number of offspring produced by their relatives. Consequently, costly altruism can evolve even if it has a net negative effect on the average reproductive success of related recipients. The selective pressure on volatility-suppressing altruism is proportional to the coefficient of variation in population fitness, and is therefore diminished by its own success. Our results formalize the hitherto elusive link between bet-hedging and altruism<sup>4,9–11</sup>, and reveal missing fitness effects in the evolution of animal societies.**

The widespread phenomenon of organisms paying costs to help others (altruism) is a long-standing paradox in biology<sup>1,2</sup>. Recently, variance-averse investment in stochastic environments (bet-hedging) has been suggested as an explanation for a number of major puzzles in the evolution of altruism, including the origins of sociality in birds<sup>9,11,12</sup>, insects<sup>13</sup> and rodents<sup>14</sup>, the altitudinal distribution of eusocial species<sup>7</sup>, and the evolution of cooperation between eusocial insect colonies<sup>15</sup>. The global distribution of animal societies is linked to environmental stochasticity<sup>4</sup>. In birds<sup>6,12</sup>, mammals<sup>16</sup>, bees<sup>7</sup> and wasps<sup>8</sup>, cooperation is more common in unpredictable or harsh environments. However, the effects of stochasticity have largely been omitted from social evolutionary theory. There are a few notable exceptions: in ref. 17 it is argued that selection will maximize expected inclusive fitness under uncertainty; ref. 18 shows that mutualism between non-relatives could counteract kin selection by dampening stochasticity; and stochastic effects on reproductive value are explored in ref. 19. However, despite speculation<sup>11,20</sup>, the proposed link between bet-hedging and altruism<sup>9</sup> has remained elusive<sup>4</sup>. We resolve this link by presenting a stochastic generalization of Hamilton’s rule (stochastic Hamilton’s rule), which predicts when organisms should pay a cost to influence the variance in the reproductive success of their relatives.

We allow the environmental state  $\pi$  to fluctuate among the possible states  $\Pi$ ; stochasticity is the condition that states are unpredictable. We follow the established method of capturing fitness effects as regression slopes<sup>1</sup>. Both the fitnesses  $w_x$  of individual organisms and the average fitness  $\bar{w}$  in the population may vary among the states  $\Pi$ . We denote the  $k$ th central moment of  $\bar{w}$  as  $\langle\langle^k\bar{w}\rangle\rangle$ . The joint distribution of the fitness of individual  $x$  ( $w_x$ ) and  $\bar{w}$  across states  $\Pi$  is captured by their mixed moments (covariance,  $k=1$ ; coskewness,  $k=2$ ; cokurtosis,  $k=3$  and so on; Supplementary Information A1). Altruists may not only alter

the expected number of offspring (mean,  $k=0$ ), but also may reduce the variation in offspring number (variance,  $k=1$ ) or increase the likelihood of large numbers of offspring (skew,  $k=2$ ). We denote the effect of the actor on the expected number of offspring of the recipient as the benefit  $b_\mu$ , the effect of the actor on its own expected number of offspring as the cost  $c_\mu$ , and relatedness as  $r$ . Likewise, we denote the effect of the actor on the  $k$ th mixed moment defining the reproductive success of the recipient as  $b_k$ , and the effect of the actor on the  $k$ th mixed moment of its own reproductive success as  $c_k$ . The stochastic Hamilton’s rule is therefore:

$$r \cdot \left( b_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} (\langle\langle^k\bar{w}\rangle\rangle b_\mu + b_k) \right) > \underbrace{c_\mu + \sum_{k=1}^{\infty} \frac{(-1)^k}{\mathbb{E}_\pi[\bar{w}]^k} (\langle\langle^k\bar{w}\rangle\rangle c_\mu + c_k)}_c \quad (1)$$

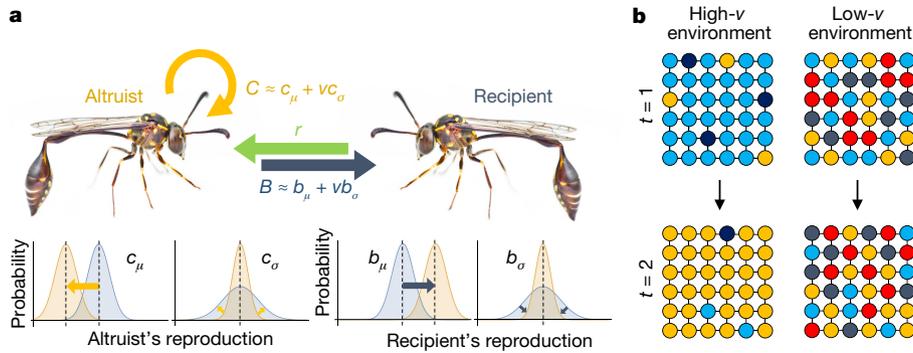
Empirical tests of Hamilton’s rule have looked for benefits and costs that constitute effects on the mean reproductive success of recipients and actors, using the form  $rb_\mu > c_\mu$  (henceforth, means-based Hamilton’s rule)<sup>21</sup>. However, equation (1) reveals that  $b_\mu$  is a single component of a range of potential benefits of altruism. Conclusions based on mean reproductive success ( $b_\mu$  and  $c_\mu$ ) overlook effects on the variance of the distribution from which a recipient samples its reproductive success.

Asocial bet-hedging has been analysed extensively<sup>3</sup>, and is typically described in terms of costs and benefits: the cost is a reduction in mean reproductive success, whereas the benefit is a reduction in the variance of reproductive success<sup>3</sup>. Following speculation that these benefits and costs could be accrued by different partners<sup>9,13</sup>—actors pay costs whereas recipients derive benefits (Fig. 1a)—we refer to decoupled benefits and costs as altruistic bet-hedging. We let  $b_\sigma$  and  $c_\sigma$  denote, respectively, the effects on the standard deviation (volatility) of the recipient and actor in reproductive success (weighted by its correlation with population average reproductive success  $\bar{w}$ ; for details see Extended Data Table 1). We introduce the stochasticity coefficient  $v$  as the coefficient of variation in  $\bar{w}$  across environmental conditions ( $v = \frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$ ; Fig. 1b). For cases in which the actor can affect both the mean and the volatility (but not higher moments) of the reproductive success of the recipient, equation (1) simplifies (Supplementary Information A2) to:

$$r(b_\mu + vb_\sigma) > c_\mu + vc_\sigma \quad (2)$$

Reducing the ( $\bar{w}$ -correlated) volatility in the recipient’s number of offspring ( $b_\sigma > 0$ ) confers on the recipient greater relative fitness in poor environmental states: extra offspring are disproportionately valuable when competitors produce few offspring<sup>22</sup>, underscoring the principle that the ultimate currency for benefits and costs under stochasticity is the expectation of relative fitness<sup>1</sup>. It is straightforward to derive the established asocial bet-hedging model<sup>3</sup> by setting  $r=0$  (Supplementary Information A3).

<sup>1</sup>School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK. <sup>2</sup>Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4QG, UK. <sup>3</sup>Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK.



**Figure 1 | Environmental stochasticity has been missing from models of social evolution.** In the means-based application of Hamilton's rule ( $rb_\mu > c_\mu$ ) to real-world organisms<sup>21</sup>, recipients gain an increase in average reproductive success ( $b_\mu > 0$ ) whereas actors suffer a decrease in average reproductive success ( $c_\mu > 0$ ). **a**, We derive an explicitly stochastic Hamilton's rule:  $r(b_\mu + \nu b_\sigma) > c_\mu + \nu c_\sigma$ . This shows that benefits can also arise by reducing the volatility of the reproductive success of the recipient ( $b_\sigma > 0$ ), which depends on the magnitude of environmental stochasticity ( $\nu$ ). An increase in the reproductive volatility of the actor ( $c_\sigma > 0$ ) imposes a cost on the actor. Each effect represents a transformation of a probability

distribution for reproductive success (bottom). Total benefits and costs ( $B$  and  $C$ ) are measured in expected relative fitness<sup>1</sup>. **b**, Environmental stochasticity ( $\nu$ ) is highest when spatial patches fluctuate in sync: for instance, if drought affects a randomly chosen patch  $Z$ , it should be likely that it also affects a randomly chosen patch  $Y$  (Supplementary Information A6). Here, following ref. 3, we represent patches in a lattice connected by dispersal. Colours denote environmental condition on patches at sequential time points  $t$ . See Supplementary Information A. Image of wasp reproduced with permission from Z. Soh.

Formally, we define altruistic bet-hedging as a reduction in the reproductive volatility of a recipient (positive  $b_\sigma$ ) that overcomes an otherwise deleterious cost to the expected reproductive success of the actor (positive  $c_\mu$ ). Strong benefits can arise when  $b_\mu$  and  $b_\sigma$  are both positive, and reductions in the actor's own reproductive volatility ( $c_\sigma < 0$ ) diminish total costs (Fig. 2a, b). Moreover, when  $b_\sigma > c_\sigma$ , increasing stochasticity reduces the minimum relatedness ( $r$ ) required for altruism to evolve (Fig. 2c). Fluctuations in relatedness ( $r$ ) alter selection only if they correlate with strong fluctuations in population average reproductive success ( $\bar{w}$ ) (Supplementary Information A4).

We note four predictions of the stochastic Hamilton's rule that differ from standard expectations:

(i) Selection can favour altruism ( $C > 0$ ) with zero increase to the expected reproductive success of the recipient ( $b_\mu = 0$ ). Such a seemingly paradoxical lack of benefits is observed in cases for which additional helpers appear redundant<sup>23</sup>. Paradoxical helpers can be selected for by reducing the reproductive volatility of the recipient if:

$$rb_\sigma > \frac{c_\mu}{\nu} + c_\sigma$$

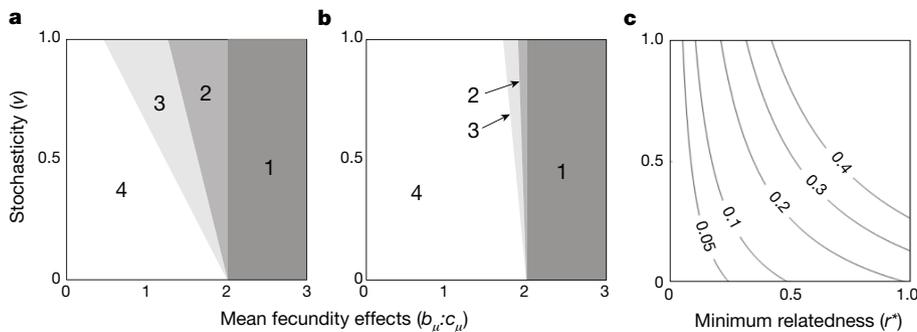
(ii) Actors may be selected to harm the expected reproductive success of their relatives ( $b_\mu < 0, c_\mu > 0$ ). The harm is outweighed by a reduction in the reproductive volatility of the recipient (Fig. 2) if:

$$rb_\sigma > \frac{c_\mu - rb_\mu}{\nu} + c_\sigma$$

(iii) Altruists that reduce the reproductive volatility of their recipients can be favoured by selection in the absence of environmental stochasticity, but only when population size ( $N$ ) is low (in extremely small populations<sup>3</sup> or small demes with intense local competition<sup>24</sup>) and  $b_\sigma^2 > c_\sigma^2$ . Effects on variance,  $\sigma^2$ , not volatility, are used here for notational convenience (Supplementary Information A5):

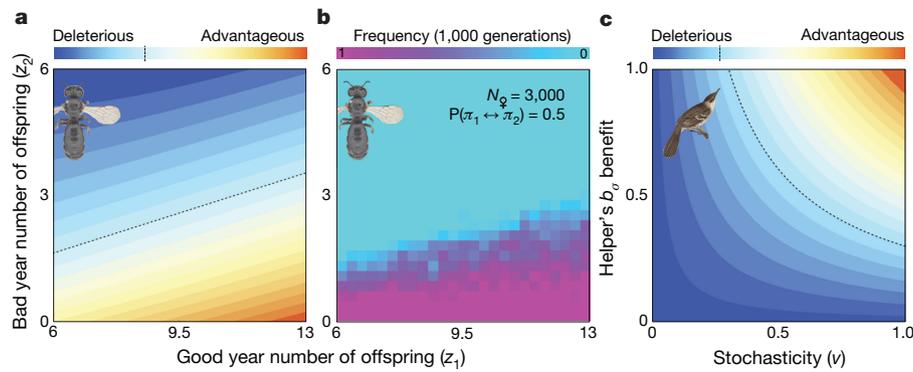
$$r \left( b_\mu + \frac{b_\sigma^2}{N \mathbb{E}_\pi[\bar{w}]} \right) > c_\mu + \frac{c_\sigma^2}{N \mathbb{E}_\pi[\bar{w}]} \tag{3}$$

(iv) Very strong altruistic effects ( $b_\sigma \gg 0$ ) can undermine the success of the altruist genotype (Extended Data Fig. 1; Supplementary Information B1–B4). Altruists that substantially reduce the



**Figure 2 | Increased stochasticity can increase the potential for selection of altruistic behaviour.** Without stochastic effects, altruism evolves when  $rb_\mu > c_\mu$  (shown in region '1' in **a** and **b** for  $c_\mu = 1$ , and  $r = 0.5$ ). As stochasticity  $\nu$  increases, the power of  $b_\sigma:c_\sigma$  benefits increases, reducing the ratio of  $b_\mu:c_\mu$  needed for the evolution of altruism. **a**, In this scenario, altruists secure a high  $b_\sigma = 0.75$ , considerably increasing the scope for altruism (extending region '1' to region '2'). Actors may also reduce the volatility of their personal fecundity (here,  $c_\sigma = -0.4$ ), reducing the magnitude of the total cost  $C$  below  $c_\mu$  and increasing the potential for

altruism further (extending to region '3'). Altruism is always deleterious in region '4'. **b**, In this scenario, altruists secure a low  $b_\sigma = 0.1$  and personal volatility reduction of  $c_\sigma = -0.1$  (regions as in **a**). Comparing **a** ( $b_\sigma = 0.75$ ) and **b** ( $b_\sigma = 0.1$ ), larger reductions of recipient volatility (higher  $b_\sigma$ ) result in larger increases in the inclusive fitness of the actor. **c**, The minimum relatedness required for the evolution of altruism under different  $c_\mu$  values (curved lines, from  $c_\mu = 0.05$  to  $0.4$ , when  $b_\sigma = 0.75, c_\sigma = 0$  and  $b_\mu = 0.2$ ); as stochasticity ( $\nu$ ) increases, the minimum required relatedness ( $r^*$ ) decreases.



**Figure 3 | Empirical studies of Hamilton's rule may benefit from incorporating stochasticity.** **a**, Model of sister–sister cooperation between facultatively social insects: the means-based Hamilton's rule ( $rb_{\mu} > c_{\mu}$ ) is violated throughout the plot. Despite this, in the region below the dashed line (which denotes  $rB = C$ ), volatility effects can favour the invasion of nonreproductive altruists. **b**, These predictions are matched in an individual-based haplodiploid simulation. In both **a** and **b**, good and bad years occur equally ( $d_{\pi} = 0.5$ ) at random. When benefits are slight (close to the dashed line in **a**), chance correlated fluctuations can drive cooperators extinct. In Supplementary Information B, we discuss temporal

correlation. Coordinates plot average frequency across five replicate simulations after 1,000 generations, from an initial frequency  $P = 0.05$ . **c**, In high-stochasticity conditions, helpers may buffer breeders from profound environmental fluctuations<sup>4,9,11</sup>. We estimate  $rb_{\mu}$  values in the Galapagos mockingbird, and show that volatility effects can, in principle, drive cooperation (above the dashed line) even when mean fecundity costs  $c_{\mu}$  cancel out  $b_{\mu}$  (here,  $b_{\mu} = c_{\mu} = 0.3$ ). See Supplementary Information C. Image of bee, K. Walker (CC-BY 3.0 AU); image of mockingbird, Biodiversity Heritage Library (CC-BY 2.0).

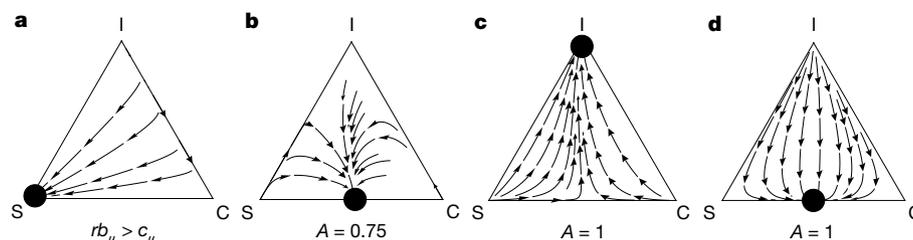
reproductive volatility of their recipients spread rapidly. As successful altruists reach high frequencies, the coefficient of variation in average reproductive success ( $v = \frac{\sigma_{\pi}[\bar{w}]}{\mathbb{E}_{\pi}[\bar{w}]}$ ) tends towards zero (Extended Data Fig. 2). When  $v$  is small, any  $b_{\sigma}$  has a small effect (equation (2)), so altruistic bet-hedgers undermine the condition (high  $v$ ) that favoured them (Extended Data Fig. 1a, b). This frequency dependence can generate a mixed population of altruists and defectors (Extended Data Fig. 1c), provided that allele frequency does not fluctuate intensively, which can otherwise destabilize the equilibrium (Extended Data Fig. 3) and lead to fixation<sup>25</sup>.

Apparent reduction of the reproductive volatility of recipients (implying  $b_{\sigma} > 0$ ) has been shown in starlings<sup>9</sup>, sociable weavers<sup>26</sup>, woodpeckers<sup>10</sup>, wasps<sup>27</sup> and allodapine bees<sup>13</sup>. We illustrate a volatility-reduction route to sociality with two examples. First, we consider sister–sister cooperation in facultatively social insects (as in certain carpenter bees, for which a means-based Hamilton's rule is violated<sup>28</sup>). In strongly stochastic environments, altruism can evolve between haplodiploid sisters when values of mean fecundity alone would predict it to be deleterious, as predicted by equation (2) (Fig. 3a) and simulations of haplodiploid populations (Fig. 3b; Supplementary

Information C1). Second, using published estimates of mean fecundity and high stochasticity in Galapagos mockingbirds (*Mimus parvulus*), we indicate how volatility effects could favour cooperative breeding even if helping increases the average fecundity of the recipient only as much as it reduces that of the actor ( $c_{\mu} = b_{\mu}$ ; Fig. 3c; Supplementary Information C2).

Equation (2) reveals three core conditions for altruistic bet-hedging. First, members of the non-altruistic genotype suffer synchronous fluctuations in lifetime reproductive success driven by environmental state (high  $v$ ) that can be stabilized by sociality ( $b_{\sigma} > 0$ ). Second, relatedness ( $r$ ) is above the threshold  $r^* = \frac{c_{\mu} + vc_{\sigma}}{b_{\mu} + vb_{\sigma}}$ . Third, actors either cannot predict environmental fluctuations or cannot generate phenotypes for different conditions (Fig. 4; Supplementary Information B5). If actors can obtain and utilize information at sufficiently low costs (rendering the environment predictable), plastic cooperation outcompetes constitutive cooperation (increasing  $b_{\mu}$  and reducing  $c_{\mu}$ ).

Synchronous fluctuations (high  $v$ ) are generated when different patches within the population experience correlated environmental changes (Fig. 1b; Supplementary Information A6). If offspring disperse across environmentally uncorrelated patches<sup>3</sup> but compete



**Figure 4 | The trade-off between constitutive and inducible altruism in a stochastic world depends on plasticity costs and information reliability.** We show a population fluctuating randomly between a good and a bad environmental state, comprising three alleles: 'selfish' (S), for which the carriers never cooperate; 'constitutive cooperator' (C), for which the carriers always cooperate; and 'inducible cooperator' (I) for which the carriers cooperate only when they believe they are in the bad (low-fecundity) state. Information reliability is set by  $A$  (actors diagnose true state with probability  $A$ ). Apexes represent monomorphic populations. Without social behaviour, individuals obtain four and one offspring in good and bad states respectively. Cooperation confers on recipients 1.5 additional offspring in bad states but reduces recipient fecundity by 0.2 offspring in good states, and costs actors 0.5 offspring in all states.

**a**, When considering only mean fecundity, the means-based Hamilton's rule  $rb_{\mu} > c_{\mu}$ , commonly used empirically, mistakenly predicts that selfishness (S) will dominate. Under stochastic conditions, cooperation evolves. **b**, Constitutive cooperators invade (until reaching a mixture of altruists and defectors) when information is imperfect ( $A = 0.75$ ) and there is a plasticity cost (0.1 offspring). **c**, When the reliability of information is increased ( $A = 1$ ), plastic cooperators outcompete constitutive cooperators. **d**, Increasing plasticity costs, however (here, from 0.1 to 0.3 offspring), eliminates plasticity benefits, enabling constitutive cooperators to invade. Vectors show directions of expected changes in frequencies: these represent continuous expected trajectories when frequencies are constrained to change by small amounts per generation. Relatedness  $r = 0.5$  in all plots. Details are provided in Supplementary Information B.

at a whole-population level,  $\nu$  decreases. Likewise, iteroparity and long generations across different environmental conditions reduce  $\nu$ , whereas correlated exposure to environmental conditions within lifetimes increases  $\nu$ . For these reasons, equation (2) suggests that the most promising avenues to detect  $b_{\sigma}$ -driven sociality may occur among social microbes, which can experience population-wide fluctuations (high  $\nu$ ), short generations (high  $\nu$ ), competing clones (high  $r$ ), and opportunities to confer homeostasis on others ( $b_{\sigma} > 0$ ), including through the construction of biofilms<sup>29</sup> and incipiently-multicellular clusters withstanding profound abiotic and biotic stress.

We have shown that altruistic effects on recipient volatility are visible to selection. Notably, Hamilton's rule identifies ultimate payoffs by incorporating any effects of population structure<sup>1</sup>. To make case-specific predictions, researchers should, accordingly, utilize explicit information on population structure and ecology. The empirical challenge to detect volatility-suppressing sociality in wild organisms will best be met using tailored models guided by field data for specific scenarios, led by the general framework of inclusive fitness theory<sup>1,21,30</sup>. In summary, Hamilton's rule reveals the action of selection under stochasticity: shielding relatives from a volatile world can drive the evolution of sociality.

**Code Availability** Simulation output was generated using MATLAB code provided in section D of the Supplementary Information; this is also available from the corresponding author upon reasonable request.

**Data Availability** The data that support the findings of this study are available from the corresponding author upon reasonable request.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

**Received 18 July 2017; accepted 1 February 2018.**

**Published online 7 March 2018.**

- Gardner, A., West, S. A. & Wild, G. The genetical theory of kin selection. *J. Evol. Biol.* **24**, 1020–1043 (2011).
- Hamilton, W. D. The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16 (1964).
- Starrfelt, J. & Kokko, H. Bet-hedging—a triple trade-off between means, variances and correlations. *Biol. Rev. Camb. Phil. Soc.* **87**, 742–755 (2012).
- Cockburn, A. & Russell, A. F. Cooperative breeding: a question of climate? *Curr. Biol.* **21**, R195–R197 (2011).
- Rubenstein, D. R. & Lovette, I. J. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419 (2007).
- Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78 (2011).
- Kocher, S. D. *et al.* Transitions in social complexity along elevational gradients reveal a combined impact of season length and development time on social evolution. *Proc. R. Soc. Lond. B* **281**, 20140627 (2014).
- Sheehan, M. J. *et al.* Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.* **18**, 1057–1067 (2015).
- Rubenstein, D. R. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl Acad. Sci. USA* **108**, 10816–10822 (2011).
- Koenig, W. D. & Walters, E. L. Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker. *Proc. R. Soc. Lond. B* **282**, 20151742 (2015).
- Shen, S., Emlen, S. T., Koenig, W. D. & Rubenstein, D. R. The ecology of cooperative breeding behaviour. *Ecol. Lett.* **20**, 708–720 (2017).
- Griesser, M., Drobniak, S. M., Nakagawa, S. & Botero, C. A. Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* **15**, e2000483 (2017).

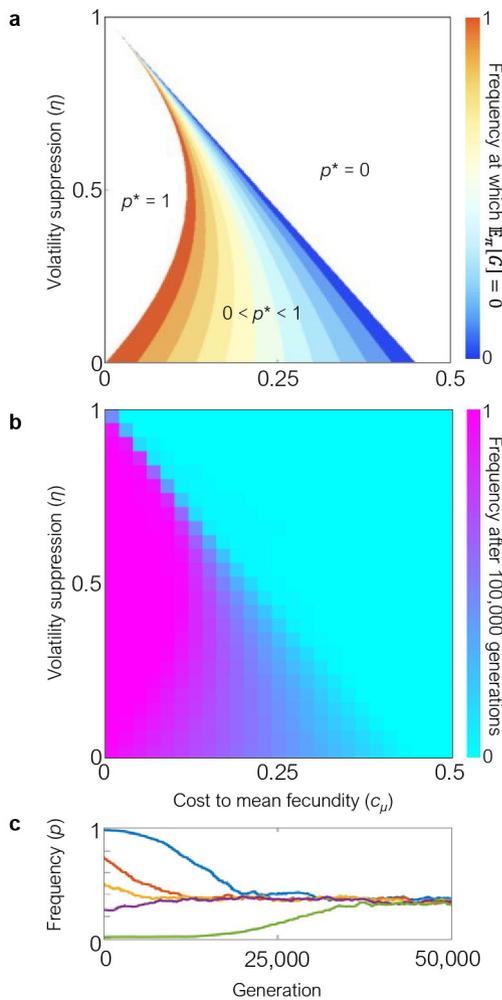
- Stevens, M. I., Hogendoorn, K. & Schwarz, M. P. Evolution of sociality by natural selection on variances in reproductive fitness: evidence from a social bee. *BMC Evol. Biol.* **7**, 153 (2007).
- Ebensperger, L. A. *et al.* Mean ecological conditions modulate the effects of group living and communal rearing on offspring production and survival. *Behav. Ecol.* **25**, 862–870 (2014).
- Sumner, S., Lucas, E., Barker, J. & Isaac, N. Radio-tagging technology reveals extreme nest-drifting behavior in a eusocial insect. *Curr. Biol.* **17**, 140–145 (2007).
- Lukas, D. & Clutton-Brock, T. Climate and the distribution of cooperative breeding in mammals. *R. Soc. Open Sci.* **4**, 160897 (2017).
- Grafen, A. Optimization of inclusive fitness. *J. Theor. Biol.* **238**, 541–563 (2006).
- Uitendhaag, J. C. M. Bet hedging based cooperation can limit kin selection and form a basis for mutualism. *J. Theor. Biol.* **280**, 76–87 (2011).
- Lehmann, L. & Rousset, F. The genetical theory of social behaviour. *Philos. Trans. R. Soc. Lond. B* **369**, 1–18 (2014).
- Koenig, W. D., Dickinson, J. L. & Emlen, S. T. in *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (eds Koenig, W. D. & Dickinson, J. L.) 353–374 (Cambridge Univ. Press, 2016).
- Bourke, A. F. G. Hamilton's rule and the causes of social evolution. *Phil. Trans. R. Soc. Lond. B* **369**, 20130362 (2014).
- Grafen, A. Developments of the Price equation and natural selection under uncertainty. *Proc. R. Soc. Lond. B* **267**, 1223–1227 (2000).
- Dickinson, J. L. & Hatchwell, B. J. in *Ecology and Evolution of Cooperative Breeding in Birds* (eds Koenig, W. D. & Dickinson, J. L.) 48–66 (Cambridge Univ. Press, 2004).
- Lehmann, L. & Balloux, F. Natural selection on fecundity variance in subdivided populations: kin selection meets bet hedging. *Genetics* **176**, 361–377 (2007).
- Lande, R. Expected relative fitness and the adaptive topography of fluctuating selection. *Evolution* **61**, 1835–1846 (2007).
- Covas, R., du Plessis, M. A. & Doutrelant, C. Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* **63**, 103–112 (2008).
- Wenzel, J. W. & Pickering, J. Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl Acad. Sci. USA* **88**, 36–38 (1991).
- Rehan, S. M., Richards, M. H., Adams, M. & Schwarz, M. P. The costs and benefits of sociality in a facultatively social bee. *Anim. Behav.* **97**, 77–85 (2014).
- Lowery, N. V., McNally, L., Ratcliff, W. C. & Brown, S. P. Division of labor, bet hedging, and the evolution of mixed biofilm investment strategies. *MBio* **8**, e00672-17 (2017).
- Birch, J. The inclusive fitness controversy: finding a way forward. *R. Soc. Open Sci.* **4**, 170335 (2017).

**Supplementary Information** is available in the online version of the paper.

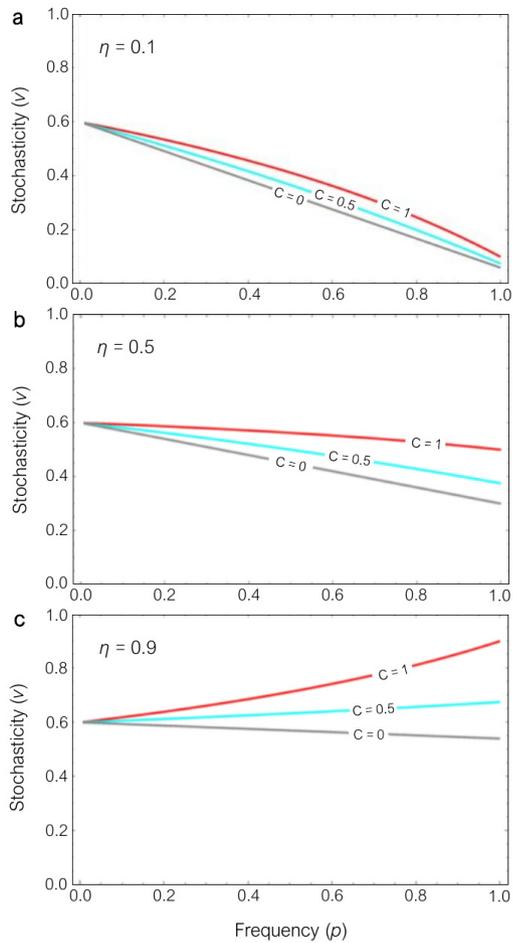
**Acknowledgements** We thank A. Gardner for discussions in the early stages of this work, and P.K. thanks the Behaviour Discussion Group at the Smithsonian Tropical Research Institute in Panama for the opportunity to present and discuss these ideas. We thank S. Schindler, S. Okasha, B. Autzen, J. McNamara and M. Bentley for comments on the project. P.K. was supported by the National Geographic Society (GEF-NE 145-15) and a University of Bristol Research Studentship, A.D.H. by the Natural Environment Research Council (NE/L011921/1), A.N.R. by a European Research Council Consolidator Grant (award no. 682253) and S.S. by the Natural Environment Research Council (NE/M012913/2).

**Author Contributions** P.K. conceived the idea, P.K. and A.D.H. performed the modelling, A.N.R. and S.S. supervised the project. All authors discussed the ideas and wrote the manuscript.

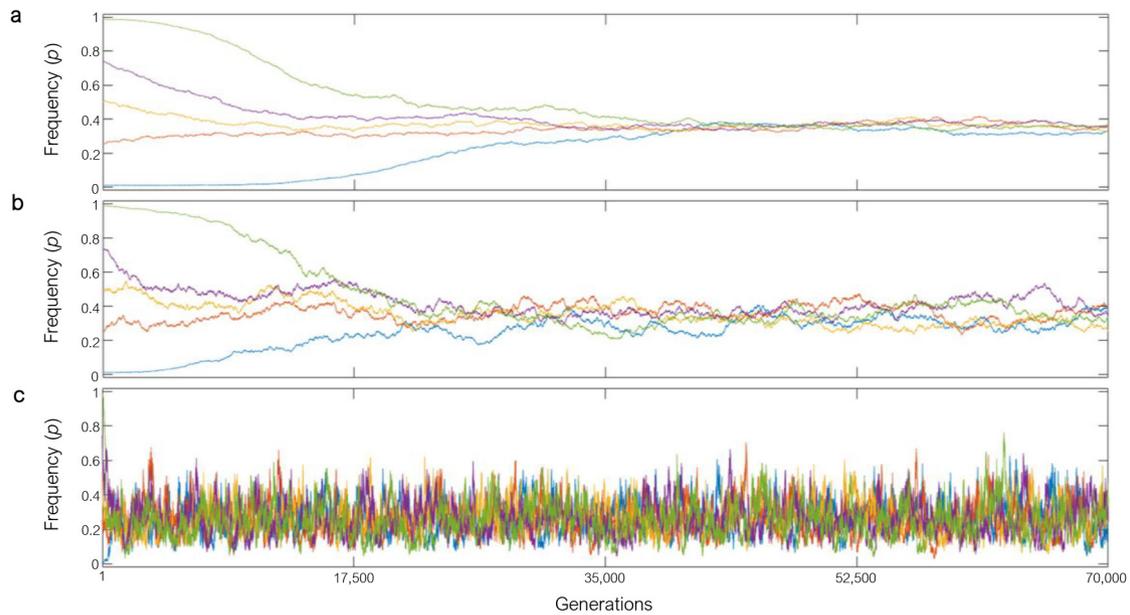
**Author Information** Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to P.K. ([patrick.c.kennedy@live.co.uk](mailto:patrick.c.kennedy@live.co.uk)).



**Extended Data Figure 1 | The interaction between the frequency of altruists and the effectiveness of altruism.** **a**, The stochastic Hamilton's rule predicts that selection on volatility-suppressing altruism with fixed costs and benefits can generate negative frequency dependence and is sensitive to mild mean-fecundity costs ( $c_\mu$ ). Lower values of  $\eta$  denote greater buffering of recipients from the environment. We evaluate a population undergoing synchronous fluctuations to identify the frequency  $p^*$  at which there is no expected change in allele frequency. We illustrate the result with individual fecundities in good years ( $z_1$ ) of four offspring and in bad years ( $z_2$ ) of one offspring. Relatedness is  $r = 0.5$ . **b**, Simulated population outcomes (frequency after 100,000 generations) match predictions of the stochastic Hamilton's rule in **a**. Warmer colours (pink) denote higher polymorphic frequencies of altruists. In this haploid model (Supplementary Information B1-4), 1% of breeding spots are available each year for replacement by offspring that year: with such constraints on the magnitude of the response to selection, radical stochastic shifts in allele frequency over single generations do not occur, allowing the population to settle at equilibria where all alleles have equal expected relative fitness without being continually displaced (Extended Data Fig. 3). **c**, Competing an altruistic allele against a defector allele reveals the action of frequency-dependent selection. Here, populations experiencing costs of  $c = 0.2$  and  $\eta = 0.466$  converge to  $p^* = 0.359$  from any initial frequency (coloured lines show five starting frequencies from 0.001 to 0.999), as predicted by the stochastic Hamilton's rule.



**Extended Data Figure 2 | Stochasticity as a function of bet-hedger frequency.** Stochasticity  $v = \frac{(p\eta + (1-p))\sigma_{00}}{\mu_{00} - pc}$  for the model of altruistic bet-hedging in Supplementary Information B plotted against frequency ( $p$ ) and cost ( $c$ ) for three different values of  $\eta$ . **a, b**, When  $\eta$  is small, representing high levels of volatility suppression,  $v$  declines steeply with  $p$  across the range of costs. **c**, When  $\eta$  is large, the sign of the effect of  $p$  on  $v$  depends on  $c$ . Values of other parameters:  $z_1 = 4$ ,  $z_2 = 1$ , and frequency of good years  $d = 0.5$ .



**Extended Data Figure 3 | Weak selection negates the capacity of temporal autocorrelation to drive the frequency of altruistic bet-hedgers away from the convergence frequency.** Individual-based simulations from five different initial frequencies of an altruistic bet hedging allele ( $p$ ) competing against a non-cooperator. **a**, The population has zero temporal autocorrelation (environmental state in each generation is random). **b**, The population has strong temporal autocorrelation (environmental state in the next generation has a 90% probability of remaining the same as in the current generation). Despite higher

amplitude fluctuations, this population converges to the same point (from the five different starting frequencies) as the uncorrelated population (**a**). **c**, The same population is simulated with greater gene frequency changes (10% of the resident genotype frequencies are available to change each generation). The population is repeatedly carried to frequencies far from the convergence point. In this case, the utility of the stochastic Hamilton's rule is both identifying whether a given trait is immune from invasion by competitors, and identifying the expected generational change at each frequency  $p$ . Parameters are  $z_1 = 4$ ,  $z_2 = 1$ ,  $r = 0.5$ .

Extended Data Table 1 | Parameters of the model

Notation	Definition	Expression
$N$	Population size	–
$w_x$	Number of surviving offspring (reproductive success) of the $x$ th individual	–
$\bar{w}$	Mean reproductive success in the population	–
$\pi$	Environmental state within the set of states $\Pi$	–
$G_x$	Genetic value of individual $x$	–
$r$	Relatedness	$\beta_{G_y, G_x}$
$z_x$	Trait value of individual $x$	–
$\ll^k \bar{w} \gg$	$k$ th central moment of $\bar{w}$ across $\Pi$	$\mathbb{E}_\pi[(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k]$
$\ll w_x,^k \bar{w} \gg$	$k$ th mixed moment of reproductive success of individual $x$ and $\bar{w}$ across $\Pi$	$\mathbb{E}_\pi[(w_x - \mathbb{E}_\pi[w_x])(\bar{w} - \mathbb{E}_\pi[\bar{w}])^k]$
$v$	Stochasticity of the environment	$\frac{\sigma_\pi[\bar{w}]}{\mathbb{E}_\pi[\bar{w}]}$
$\rho_x$	Correlation between $w_x$ and $\bar{w}$ across $\Pi$	$\frac{\mathbb{E}_\pi[w_x \bar{w}] - \mathbb{E}_\pi[w_x] \cdot \mathbb{E}_\pi[\bar{w}]}{\sigma_\pi[w_x] \sigma_\pi[\bar{w}]}$
$B$	Total benefit in Hamilton’s rule under stochasticity	$\beta_{\mathbb{E}_\pi[\frac{w_y}{\bar{w}}], G_x}$ Partial regression of a focal individual’s genetic value on a social partner’s expected relative fitness
$C$	Total cost in Hamilton’s rule under stochasticity	$-\beta_{\mathbb{E}_\pi[\frac{w_x}{\bar{w}}], G_x}$ Partial regression of a focal individual’s genetic value on its own expected relative fitness
$b_\mu$	Mean fecundity benefit in stochastic Hamilton’s rule	$\beta_{\mathbb{E}_\pi[w_y], G_x}$ Partial regression of a focal individual’s genetic value on a social partner’s expected number of offspring. We make use of the identity $\beta_{\mathbb{E}_\pi[w_y], G_x} = \beta_{\mathbb{E}_\pi[w_x], G_y}$ in non-class-structured populations.
$c_\mu$	Mean fecundity cost in stochastic Hamilton’s rule	$-\beta_{\mathbb{E}_\pi[w_x], G_x}$ Partial regression of a focal individual’s genetic value on its own expected number of offspring
$b_\sigma$	Volatility-suppressing benefit in stochastic Hamilton’s rule	$-\beta_{\rho \sigma_\pi[w_y], G_x}$ Partial regression of a focal individual’s genetic value on a partner’s standard deviation in reproductive success, where the standard deviation is weighted by its correlation with $\bar{w}$ . We make use of the identity $\beta_{\rho \sigma_\pi[w_y], G_x} = \beta_{\rho \sigma_\pi[w_x], G_y}$ in non-class-structured populations
$c_\sigma$	Volatility-suppressing cost in stochastic Hamilton’s rule	$\beta_{\rho \sigma_\pi[w_x], G_x}$ Partial regression of a focal individual’s genetic value on a partner’s standard deviation in reproductive success, where the standard deviation is weighted by its correlation with $\bar{w}$
$b_k$	$k$ th moment benefit in stochastic Hamilton’s rule	$\beta_{\ll w_y,^k \bar{w} \gg, G_x}$ Partial regression of a focal individual’s genetic value on the $k$ th mixed moments of a partner’s joint distribution for reproductive success $w_y$ and population average reproductive success $\bar{w}$ . We make use of the identity $\beta_{\ll w_x,^k \bar{w} \gg, G_y} = \beta_{\ll w_y,^k \bar{w} \gg, G_x}$ in non-class-structured populations
$c_k$	$k$ th moment cost in stochastic Hamilton’s rule	$-\beta_{\ll w_x,^k \bar{w} \gg, G_x}$ Partial regression of a focal individual’s genetic value on the $k$ th mixed moments of its own joint distribution for reproductive success $w_x$ and population average reproductive success $\bar{w}$ .

For derivation of regression slopes, see Supplementary Information A.

## Life Sciences Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form is intended for publication with all accepted life science papers and provides structure for consistency and transparency in reporting. Every life science submission will use this form; some list items might not apply to an individual manuscript, but all fields must be completed for clarity.

For further information on the points included in this form, see [Reporting Life Sciences Research](#). For further information on Nature Research policies, including our [data availability policy](#), see [Authors & Referees](#) and the [Editorial Policy Checklist](#).

### ▶ Experimental design

#### 1. Sample size

Describe how sample size was determined.

Not applicable (data are simulation output)

#### 2. Data exclusions

Describe any data exclusions.

Not applicable.

#### 3. Replication

Describe whether the experimental findings were reliably reproduced.

Not applicable.

#### 4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Not applicable.

#### 5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Not applicable.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

#### 6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a | Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g.  $P$  values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

## ► Software

Policy information about [availability of computer code](#)

### 7. Software

Describe the software used to analyze the data in this study.

Simulations were conducted in MATLAB on a High Performance Computing unit at the University of Bristol.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

## ► Materials and reagents

Policy information about [availability of materials](#)

### 8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

Not applicable.

### 9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

Not applicable.

### 10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

Not applicable.

b. Describe the method of cell line authentication used.

Not applicable.

c. Report whether the cell lines were tested for mycoplasma contamination.

Not applicable.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

Not applicable.

## ► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

### 11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

Not applicable.

Policy information about [studies involving human research participants](#)

### 12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

Not applicable.